Dunn, G.A.

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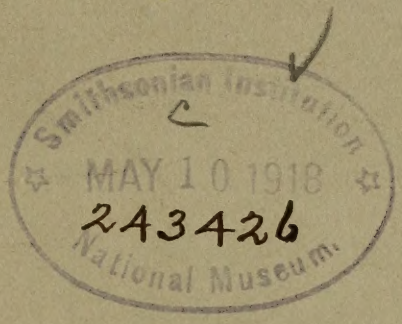
DISSERTATION

SUBMITTED TO THE BOARD OF UNIVERSITY STUDIES OF THE JOHNS HOPKINS UNIVERSITY IN CONFORMITY WITH THE REQUIREMENTS FOR THE DEGREE OF DOCTOR OF PHILOSOPHY

BY

GRACE A. DUNN



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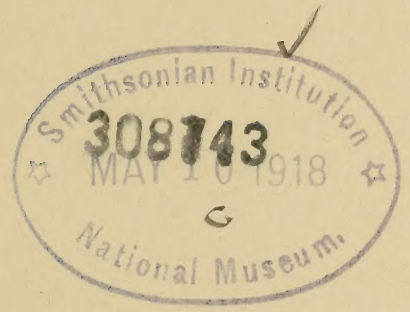

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THE
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DEVELOPMENT OF DUMONTIA FILIFORMIS[1]

II. DEVELOPMENT OF SEXUAL PLANTS AND GENERAL DISCUSSION OF RESULTS[2]

GRACE A. DUNN

(WITH PLATES XIX–XXII AND SEVEN FIGURES)

Introduction

Dumontia filiformis (Huds.) Grev. is a red seaweed which is widely scattered in the temperate zones. It has been reported as occurring on the Auckland and Falkland Islands (2), on the shores of Alaska, and is very common in northern Europe. This species was first found on the Atlantic coast of North America, by the writer, at South Harpswell, Maine, in June 1913. Tetrasporic and cystocarpic plants were collected at that time. Sterile plants were collected by THAXTER at Kittery Point, Maine, in April 1914.[3] These are the only two points on this coast where plants of *Dumontia* have been reported to occur.

In all probability *Dumontia* has become established on the coast at South Harpswell some time between 1909–1913. F. S. COLLINS collected at South Harpswell in the early part of July for 6 years (1902–1905 and 1908–1909) in the same pools in which *Dumontia* was abundant in July 1913 and 1914. He states that he has never found a single specimen of *Dumontia* in any of these pools, and if

[1] Botanical contribution from the Johns Hopkins University, no. 55.

[2] First paper entitled "The development of the tetraspores." Plant World, **19**: 271–281. *figs.* 2. 1916.

[3] Personal letter from F. S. COLLINS.

the plants were then present they must have been extremely scarce. The plants were very abundant in the early part of July 1913. If a few solitary plants were present in 1909, it is apparent that they must have multiplied rapidly in the following 4 years. It is highly improbable, therefore, that any plants of *Dumontia* were present at South Harpswell as early as 1905.

GREVILLE (1) in 1830 described fructifications which he had observed in *Dumontia filiformis*. These fructifications were attached to the inner surface of the wall of the thallus and consisted of "clusters of large ovate seeds." It is evident from GREVILLE's description and figures that these "seeds" were carpospores. KÜTZING (5) published illustrations and a very brief description of the tetraspores. HARVEY (2) pictures a group of carpospores and states that "clustered spores are common." THURET (17) refers to the antheridia of *Dumontia*, so at that time these bodies were known to exist. The writer has not been able to find any description of the antheridia. All the papers published on the red algae previous to 1883 dealt chiefly with the distribution and seasonal occurrence of the various genera and the gross morphology of the individuals. SCHMITZ's (13) paper in 1883 marks a greater step in advance in the study of the red algae than has since been made by any one investigator. Although his descriptions are not complete, his general conception of the structure of the female reproductive organs of *Dudresnaya*, *Gloeosiphonia*, and other members of the Cryptonemiales is essentially correct in regard to the cell history. His observations on *Dudresnaya*, *Polyides*, and *Petrocelis* concerning the behavior of the nuclei in the ooblastema filaments and auxiliary cells are correct. In *Gloeosiphonia* and some other genera SCHMITZ reports that the nucleus in the cell which forms the carpospores is the product of two fusions.

The structure of the female reproductive organs of the red algae is quite complicated. The auxiliary cell, the cell which produces the carpospores, in nearly all the genera is formed by the fusion of the cytoplasm of two or more cells. The behavior of the nuclei in these cells fusing to form the auxiliary cell proved to be a stumbling block to SCHMITZ and many other workers, some of whom regarded the nucleus in this cell as the product of as many as 6 fusions (HAUPT-

FLEISCH 4). The next epoch making paper in the study of the red algae was that by OLTMANNS (9). OLTMANNS worked out very carefully and in much detail the nuclear and cell history during fertilization and carpospore formation in *Dudresnaya*, *Gloeosiphonia*, and *Dasya*. OLTMANNS' chief contribution was the convincing evidence that the nucleus functioning in the auxiliary cell at the time of the formation of the carpospores is a descendant of the fusion nucleus in the carpogonium, and that no other nuclear fusion has occurred. OLTMANNS' descriptions are detailed and his illustrations are remarkably clear, but nevertheless some present day botanists question his observations concerning the absence of a fusion between the nucleus in the auxiliary cell and that nucleus which enters it from the sporogenous filament. These botanists are inclined to believe that in the members of the Crytonemiales, as in certain of the Ascomycetes, there are two nuclear fusions at the time of fertilization. *Dumontia* and *Dudresnaya* belong to the same family, Dumontiaceae, and it is to be expected therefore that the two genera will have similar reproductive organs. In view of the fact that OLTMANNS' results have been questioned by some workers, the present investigation of *Dumontia filiformis* was undertaken for the purpose of gaining all possible information concerning the behavior of the nuclei during fertilization and the formation of the carpospores. It was also desired to gain information concerning the general structure of this alga, the cytology of its tetraspores, and the structure of its male reproductive organs.

This study was begun in June 1913, at the Harpswell Laboratory, South Harpswell, Maine, where the plants were abundant. It was continued during 1913, 1914, and 1915 at South Harpswell and at Johns Hopkins University.

The writer wishes to thank Professor J. S. KINGSLEY for the privileges of the Harpswell Laboratory, and also Dr. M. A. HOWE and Mr. F. S. COLLINS for identifying this alga. This investigation was undertaken at the suggestion of Professor D. S. JOHNSON, under whose directions it has been carried out, and whose criticisms have been a constant source of aid. Dr. W. D. HOYT also has kindly examined many of the preparations.

Methods

Plants of this alga, either whole or cut into lengths of 5–10 mm. each, were fixed in medium chromo-acetic solution, or in Flemming's fluid, within a few minutes after being collected. As the alga is very gelatinous, great care was taken that all changes in the alcohols should be made very gradually. The material on which the alcohol was changed in 5 per cent grades showed considerably less shrinkage than that on which the changes were made in 10 per cent grades. Most of the paraffin sections used were 10 or 12 μ thick. Sections 2 μ thick were also used for cytological details. For staining, Heidenhain's iron alum hematoxylin (1 hour in alum solution, 2 hours in hematoxylin) gave the best results. Acid fuchsin and methyl green stained the spores very well, but were not satisfactory for the vegetative structure. The triple stain, safranin, gentian-violet, and orange G, was also used. The slipping from the slide of sections of material fixed in Flemming's fluid occurred somewhat frequently in consequence of bleaching the sections in hydrogen peroxide. This difficulty was finally largely overcome by dipping the slides into 0.5 per cent solution of celloidin in a mixture of equal parts of alcohol and ether.

Description

HABITAT AND APPEARANCE

Dumontia, at South Harpswell, grows in abundance in tufts in the small tide pools and also on the rocks that are exposed to the air at low water. On large round rocks which were much exposed to the surf, female and tetrasporic plants of *Dumontia* were found growing down almost to the lower limit reached by *Chondrus crispus*, that is, just below the mean low water level. There is considerable variation in the size of the plants. The larger plants were found in the more exposed places. The plants in the tide pools near the low water mark were larger than the plants in the higher pools, and the largest plants of all were those growing at low levels on the round rocks. The color of the plants varies from a rich dark red to a pale reddish yellow. Mature tetrasporic and female plants ranged in height from 4 cm. to 23 cm. There is

apparently no regular or constant system of branching, and the number of branches present is not related to the height of the plant (figs. 1–7). The plants shown in figs. 1 and 2 have almost

FIGS. 1–3.—Mature female plants showing cystocarps imbedded in thallus

the same number of branches, and their respective heights are 7 cm. and 19 cm. All the cystocarpic plants found were branched. Tetrasporic plants were found which were 12 cm. in height and

were unbranched. The female plants evidently attain practically their maximum size before the carpogonial branches are initiated. The average size of the female plants collected on April 12 was the

FIGS. 4, 5.—Mature tetrasporic plants branched and unbranched showing fraying out of thallus at apices of branches and main axis; ×0.6.

same as that of the mature cystocarpic plants collected in June. Some of these plants collected in April bore only young carpogonial branches, while others bore mature branches of this type and

auxiliary cell apparatuses in the upper portion of their thalli. Carpogonial branches therefore were probably initiated on these plants only a few days before they were collected. The average

FIG. 6.—Tetrasporic plant showing much inflated main axis and branches; ×0.5

size of the male is less than that of the female plants. The maximum height of the male plants examined was 20 cm. They could be distinguished from the young female plants only by microscopical

examination. Female plants bearing mature cystocarps can readily be distinguished from the male and tetrasporic plants because the cystocarps form protrusions in the wall of the thallus (figs. 1–3).

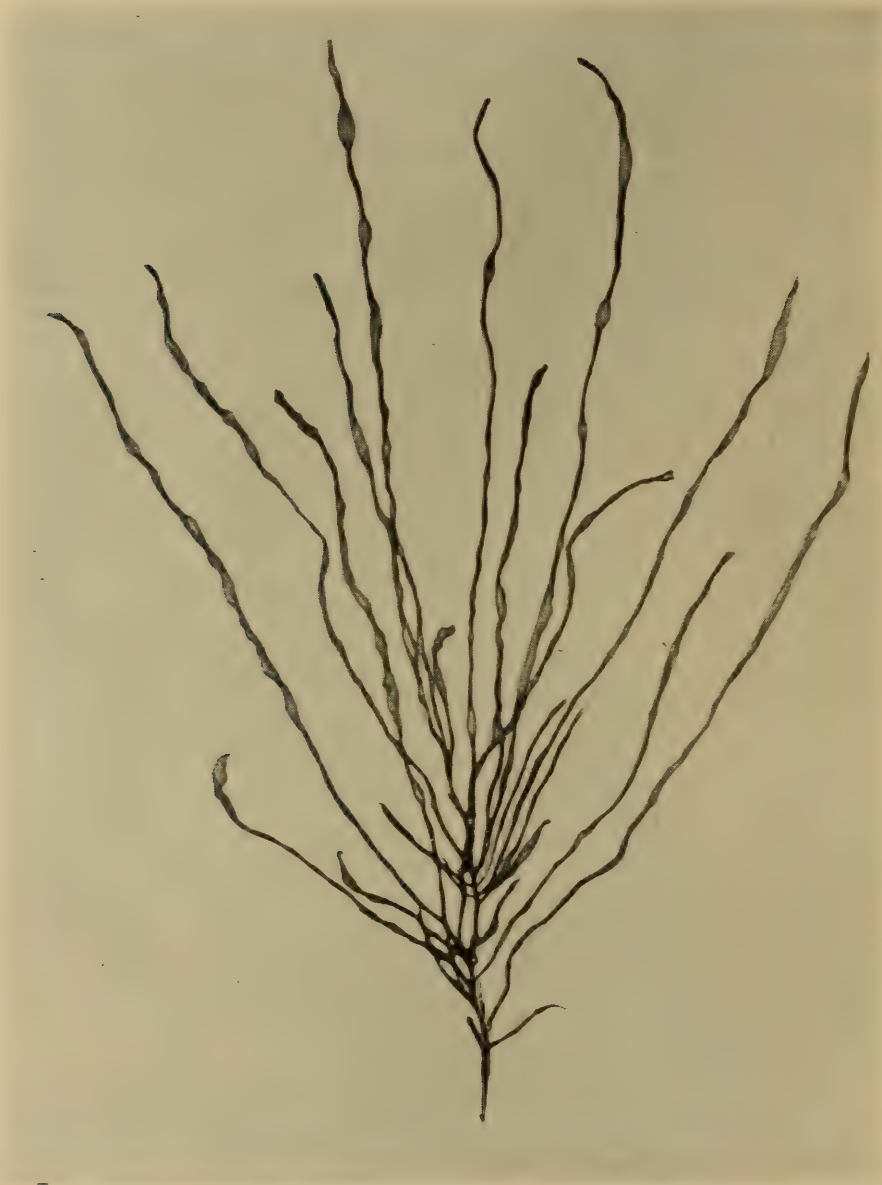

FIG. 7.—Tetrasporic plant showing large number of much twisted branches; ×0.4

The ends of the majority of plants collected in June and July were considerably frayed out (figs. 1, 3, 4, 6). Since growth is apical, the branches cannot increase greatly in length after the fraying has begun.

Lewis (8) has shown that the sexual and asexual generations in most of the Florideae at Woods Hole differ physiologically, but are identical in vegetative structure, chromosome number of course excepted. These two generations in many forms appear at different seasons and have a tendency to grow on different kinds of substrata. The plants shown in figs. 2 and 5 are fair examples of well developed cystocarpic and tetrasporic plants of *Dumontia filiformis*. It is evident from a comparison of these plants that in this species also the two generations are morphologically almost identical. The tetrasporic and cystocarpic plants of *Dumontia*, so far as substrata on which they grow are concerned, appear to be physiologically identical also. The two kinds of plants grow together on all the large rocks and in most of the tide pools. The tetrasporic plants were more abundant on the whole than the cystocarpic ones, and a few pools contained only the former. These tide pools, however, were in every instance within 3 or 4 feet of apparently similar pools on the same level, in which both kinds of plants grew. The temperature of the water was taken in a number of the pools. It was found that the temperature of pools in the same vicinity did not vary more than 2° C. This difference existed between pools which contained tetrasporic plants only, as well as between these and those pools in which both kinds of plants were present.

SEASONAL OCCURRENCE

Male and young female plants of *Dumontia* were collected in the latter part of April 1914 and on April 12, 1915. An unsuccessful search was made for plants in January 1914. It is believed that the plants were not then present. The ratio of female to male plants in the collection made in April 1914 could not be determined, owing to the fact that the plants when examined were considerably broken up. The ratio of female to male plants in the collection of April 12, 1915, was 3 to 1. This ratio is based upon the examination of 24 plants collected from several different tide pools. Another collection of plants was made on April 26, 1915, and of these plants 24 were examined, all of which proved to be female. Of these 24 plants 10 bore only carpogonial and auxiliary cell branches, while 14 bore chiefly young cystocarps and auxiliary cell branches.

There were a few plants in the collection made on April 12 which bore no reproductive organs; these were probably female plants in which the carpogonial branches had not yet been initiated. All of the plants over 4 cm. in height, collected in June and July, with the exception of 2 or 3 individuals bearing carpogonial branches, bore either mature cystocarps or tetraspores. Hundreds of plants were collected and a careful but entirely unsuccessful search was made for individuals bearing spermatia. It seems evident from these facts that the male plants are present for only 2 or 3 weeks in April. It is possible, of course, that a few solitary individuals were present in June and July. This view is supported by the fact that it was possible to find on the female plants collected during this time all stages from the 1-celled carpogonial branch to the mature cystocarps. The cystocarpic plants reach their maximum development in the early part of June and have completely disappeared by the middle of July. The tetrasporic plants attain their maximum development in the latter part of June, although plants 19 cm. in height were very abundant as early as June 12. A few tetrasporic plants persist until late in August, but they are rare even in the latter part of July. The tetrasporic and female plants in all the red algae seem to be more numerous than the male plants. The experiments of LEWIS (7) with *Griffithsia Bornetiana* and *Dasya elegans* indicate that in both of these species the tetraspores form equal numbers of male and female plants. This is probably true of *Dumontia* and other members of the Florideae. The apparent scarcity of male plants may be due to the fact that in some forms they are exceedingly small and therefore are easily overlooked. This would not apply to such forms as *Dumontia*, however, in which the difference in the average height of the male and female plants is not more than 4–5 cm. SVEDELIUS (14, 16) reports that the male plants of *Martensia* and *Delesseria* die shortly after they have discharged their spermatia. This is probably true of the *Dumontia* plants also. LEWIS (8) has found that the tetrasporic plants of most of the red algae at Woods Hole are very abundant in July. The tetraspores germinate to form cystocarpic plants from which carpospores are released in September. The holdfasts of young sporelings formed from these

carpospores persist through the winter. These holdfasts, in the following June, produce adventitious shoots which develop into tetrasporic plants. LEWIS believes that this is in general the seasonal cycle of many of the Florideae, but states that "there are also exceptions to the separation in point of time of the two generations. This separation is never of a perfectly sharp and definite character, as the generations always overlap to a certain extent in midsummer."

The seasonal cycle of *Dumontia* at South Harpswell is evidently not similar to that of the algae just mentioned. The carpospores discharged in May and June apparently develop immediately into the tetrasporic plants which are present in June and July. This seems clear from the fact that the carpospores sometimes germinate even before escaping from the cystocarp, also that young tetrasporic plants 3–7 cm. in height were often found growing beside the stumps of the frayed off cystocarpic plants. Germination of the tetraspores has not been seen, but the occurrence of only male and female plants in the spring would indicate that this species must persist through the winter in the form of sporelings derived from the tetraspores discharged in June and July.

VEGETATIVE STRUCTURE

The holdfast of *Dumontia* is a platelike body composed of a single layer of horizontal filaments, each cell of which produces an ascending, vertical branch (figs. 8, 9). These vertical branches are closely packed together, averaging about 12 cells in length, and are very regular in form and arrangement. They are generally dichotomously branched. The cells of the horizontal filaments usually form no descending branches. The few branches of this character observed consisted of only one cell (fig. 8). It is evident from the size and arrangement of the cells in the ascending branches that they develop by apical growth.

A group of vertical branches in the holdfast elongates to form the upright portion of this alga (fig. 9). In such longitudinal filaments there is a gradual increase in the length of the cells. They are closely packed together at the base of the main axis, forming a solid tissue (fig. 9). At about 0.1 mm. above the holdfast these

longitudinal filaments or medullary hyphae separate, forming a cavity which extends nearly to the tip of the plant. The thallus of the plant is thus tubular in structure. The wall consists of 3 tissue layers. The inner layer is composed of 3 or 4 vertical rows of medullary hyphae. Each cell of a medullary hypha produces a radial branch. These radial rows of cells by repeated dichotomous branching, in planes parallel and perpendicular to the surface of the thallus, form the subcortex and the cortex (fig. 10). A branch arising from a cell of a medullary hypha terminates in 64–128 cortical cells. The cells in the inner subcortex are not closely packed together. The number of cells in a given area increases as a result of the repeated branching, and thus a compact cortex is formed. The 4 figures for each cell type in the following table indicate the two diameters of the cell as seen in a longitudinal section of the thallus, also the diameters of the nucleus and nucleolus.

Medullary hyphae.....	52.2 μ	8.7 μ	2.7 μ	1.0 μ
Larger subcortical cells.....	31.5 "	21.5 "	2.7 "	1.0 "
Smaller subcortical cells....	11.2 "	9.1 "	1.8 "	0.8 "
Cortical cells.....	8.4 "	7.0 "	2.8 "	1.4 "

In addition to the radial branches forming the subcortex and cortex, the medullary hyphae may give rise to other branches which remain axial and thus form longitudinal filaments. The medullary hyphae at the tips of the branches and the main axis terminate in a number of short branches composed of small cells (fig. 11). No single initial cell could be recognized at the apex of any branch in *Dumontia*. Branches varying in length from 2 mm. to 4 cm. were examined. The structure of the apex of a branch of *Dumontia* appears to be similar to that of *Furcellaria* (WILLE 18). *Furcellaria* is cited by both WILLE and OLTMANNS as a good illustration of the "Spring-brunnen" type of vegetative structure (OLTMANNS 9). The holdfast of *Dumontia* also resembles that of *Furcellaria*. Each of the medullary hyphae in *Dumontia*, as well as each of the lateral branches arising from these hyphae, has its own initial cell. Practically all the vegetative cells of *Dumontia* are uninucleate. All the chromatin in the resting nucleus is in the nucleolus. All the vegetative cells in the thallus, with the possible exception of a

few cells in the lower layers of the holdfast, contain but one chromatophore. The chromatophore is a clathrate hollow ellipsoid lying just inside the cell wall (fig. 12). It is similar to the peripheral portion of the chromatophore figured by WOLFE (19) in *Nemalion*. The chromatophore in some cells was seen to be enveloped by a thin layer of cytoplasm in the form of a coarse net. This cytoplasmic envelope, although not always visible, was undoubtedly present in all the cells.

Intercellular connections, such as are characteristic of the Florideae, are present between all the vegetative cells and all the sexual reproductive cells, including the carpospores, until they are almost mature. At each intercellular connection there are two similar disks joined by an apparently homogeneous strand of cytoplasm. The cytoplasm appears to penetrate these disks, but the matter has not been thoroughly investigated. The disks stain readily with hematoxylin, and in some cells appear to be composed of granules (fig. 13). One case was seen in which a strand of cytoplasm 4 μ wide connects two carpospores 22 μ in diameter (fig. 14). In this strand of cytoplasm are several granules having an average length of 0.7 μ. These granules stain with the same intensity as the disks. It is probable that these granules would collect together to form the two disks when the strand of cytoplasm has assumed its normal size. Trichomes are found on all parts of the surface of the thallus. They seem to be most numerous at the base of the frond. They are present on the male, female, and tetrasporic plants. The trichomes are very abundant on the young plants collected in April.

SPERMATIA

Definition.—If the following discussion is to be intelligible, it will be necessary to define the terms which will be used in the description of the male reproductive organs. Those cells which are analogous to the sperms of the green and brown algae will be designated as spermatia. YAMANOUCHI (20), writing of *Polysiphonia*, calls these cells sperms, but "spermatia" is the term which has been most widely used by workers on the red algae and is therefore to be preferred.

SCHMITZ (13), WOLFE (19), and some other workers on the red algae have found that the spermatium is sometimes discharged as a naked protoplast. SVEDELIUS (14) therefore maintains that a distinction should be made between the free spermatium, the naked protoplast, and this same protoplast inclosed in a cell wall as it is when attached to the parent plant. He refers to the protoplast inclosed in the cell wall as the "spermatangium." The cell which SVEDELIUS refers to as the "spermatangium mother cell" is analogous to the "spermatium mother cell" of *Nemalion* (WOLFE 19).

Spermatium mother cells.—The spermatium mother cells of *Dumontia filiformis* are homologous to the outer cortical cells of the tetrasporic and cystocarpic plants. In a mature male plant of *Dumontia* almost all the outer layer of cells of all the branches and of the entire main axis from about 1 cm. above the holdfast consists of spermatia and their mother cells. The outer cortical cells of the main axis just above the holdfast are similar to those of the tetrasporic and cystocarpic plants. Although the distribution and position of the spermatium mother cells on the individuals of the different genera varies considerably, no other form has been reported in which they form a continuous layer over almost the entire thallus as they do in *Dumontia*. Each stalk cell in *Dumontia* bears at least two and probably more spermatium mother cells (fig. 15). The spermatium mother cell may bear two spermatia, just as it does in *Polysiphonia* (YAMANOUCHI 20), *Martensia* (SVEDELIUS 14), and *Delesseria* (SVEDELIUS 16).

A distinct chromatophore is certainly present in the stalk cell of the spermatium mother cell of *Dumontia filiformis* (fig. 15). A chromatophore is occasionally seen at the base of a spermatium mother cell borne on one of these stalk cells. The upper part of such a mother cell contains only granular cytoplasm (fig. 19). Many of the mother cells contain only cytoplasm and no chromatophores (fig. 15, first cell to right). Although it was not visible, a net of cytoplasm is undoubtedly present in the stalk cells as it is in all the vegetative cells of *Dumontia*. When the spermatium mother cell was first formed, it must have contained a chromatophore which had been cut off from that in the stalk cell. A large portion of the granular cytoplasm in the spermatium mother cell

was probably present originally in the chromatophore. The presence or absence of chromatophores in these cells could have been more readily determined if living plants had been available for examination. However, even in the preserved material it should be possible to distinguish the chromatophores from the cytoplasm. The protoplasm of the chromatophores is apparently homogeneous; they contain no visible vacuoles and have a definite outline. Many spermatium mother cells were seen which showed intermediate stages in the disappearance of the chromatophore and the formation of the granular cytoplasm (fig. 19).

OSTERHOUT (**11**) states that a reduced chromatophore is present in the young spermatium of *Batrachospermum*. This chromatophore disappears when the young spermatium matures. WOLFE (**19**) observed the division of the chromatophore in the spermatium mother cell of *Nemalion* in preparation for the formation of the spermatium. The chromatophore is for a time visible in the young spermatium and then disappears. Immediately after its disappearance a mass of deep staining cytoplasm is seen at one end of the spermatium. WOLFE believes that at least a portion of this cytoplasm has been derived from the protoplasm of the chromatophore. No other workers, with the possible exception of YAMANOUCHI, have seen chromatophores in the spermatia or in their mother cells. YAMANOUCHI (**20**) states that the sperm mother cells contain fine granular cytoplasm and generally no plastids. Chromatophores are present in all the genera, either in the immediate or somewhat remote ancestors of the spermatium mother cells. SVEDELIUS (**14**) states that he did not actually observe the disappearance of chromatophores in *Martensia*, but he believes that the protoplasm in the chromatophores of certain cells is used in forming the granular cytoplasm of their daughters which do not contain any chromatophores.

Spermatia.—No stages were seen showing a uninucleate spermatium mother cell. This cell in the earliest stages observed is binucleate (fig. 16). The first spermatium is cut off obliquely (figs. 15, 17, 19). The mother cell than elongates, again becomes binucleate (fig. 17), and a second spermatium is cut off. Many spermatia were seen in the swollen gelatinous sheath enveloping

the thallus and some which had actually reached the exterior (fig. 18). Every spermatium seen outside the parent plant is inclosed in a cell wall (fig. 41). No empty cell walls were seen attached to the spermatium mother cell. Many spermatia were seen lying close to the mother cells, but not attached to them (fig. 19). The spermatia in *Dumontia* are apparently cut off from the mother cell in the same manner as they are in *Polysiphonia* (YAMANOUCHI 20). The wall of the spermatium in both of these genera is a portion of the wall of the spermatium mother cell, and no body is formed which would be homologous to the spermatangium of *Delesseria* (SVEDELIUS 16). SVEDELIUS (14) believes that the spermatia in *Martensia* are set free in the same way as they are in *Polysiphonia*. LEWIS (6) states that in *Griffithsia* the spermatia are cut off from the mother cells. This form can hardly be compared with those previously mentioned, because in *Griffithsia* none of the cells of the antheridial filament form cellulose walls, but all are imbedded in the swollen wall of the mother cell of the branch.

The spermatia of *Dumontia*, as far as their contents are concerned, are similar to most of those which have been described in the other genera. The cytoplasm is much vacuolated at the proximal end of the spermatium and is very dense at the distal end. It is difficult to determine the structure of the nucleus, because it is situated at the distal end of the spermatium, imbedded in the dense, deep-staining cytoplasm. All the chromatin appears to be in the nucleolus or in several chromatin granules collected in the center of the nucleus (figs. 17, 19).

CARPOGONIAL BRANCHES

Nearly all the carpogonial branches found in the mature female plants were between the levels of 7.5 and 17.5 mm. from the holdfast. At levels higher up in the thallus, where mature cystocarps occur, a few carpogonial branches are occasionally present. These are not confined to one side of the thallus, but are scattered indiscriminately among the cystocarps. Young cystocarpic plants about 3 cm. in height were occasionally found even as late as July 5. The few cystocarps which were present on these plants were at the tips of the branches. Carpogonial branches were found in the

lower portions of the branches and in the main axis. The carpogonial branches in *Dumontia* evidently are not formed in acropetal succession. The carpogonial branches arise from the lateral branches of the medullary hyphae. They arise either from the basal cells of these subcortical branches or from cells intermediate in position between the medullary hyphae and the surface of the thallus. On the young plants every second or third large subcortical cell or occasionally each successive cell produces a carpogonial branch. Radial branches arise from the intervening cells. In mature plants, where carpogonial branches occur only at the base of the thallus, they develop from every fourth, fifth, or sixth cell. Sometimes the same cell will produce two carpogonial branches or one carpogonial branch and one radial branch (fig. 20).

A mature carpogonial branch consists of 6 or 7 cells and a trichogyne. If there are only 6 cells, they are all in a row. When the carpogonial branch is composed of 7 cells, one cell may be formed as a lateral outgrowth of the basal cell. For convenience and clearness the cells of the carpogonial branch will be numbered. The basal cell which is attached to the vegetative cell will be numbered 1, the cell above it 2, etc. The first cell of the carpogonial branches arises as a conical protrusion of the subcortical cell (fig. 21). A portion of the peripheral chromatophore of the latter is cut off in this protrusion. This first cell is uninucleate (fig. 22), and divides by a wall parallel to its base (fig. 23). The chromatophore in each of these young cells of the carpogonial branches is always peripheral, as it is in all the vegetative cells. The second cell next divides transversely, thus forming a 3-celled carpogonial branch (fig. 24). No data were obtained concerning the details of nuclear division in these earlier stages. This is due to the fact that these stages persist for only a short time, and that the cells are small and almost completely lined by the chromatophores. Considering the size and position of the cells in these young carpogonial branches, it is evident that it must be the terminal cell which divides each time. The cell wall separating the second and third cells was barely visible in some carpogonial branches which had just reached the 3-celled stage (fig. 24). These cells are separated considerably at a slightly later stage (fig. 25). In the 4-celled stage

also the 2 terminal cells are at first in close contact, but later become separated (fig. 26).

The cells of the carpogonial branch in the 4-celled stage may lie in a straight line, or the axis of the 3 terminal cells may form more or less of a right angle with that of the basal cell (figs. 27, 28). The nuclei here furnish evidence to support the assumption that the carpogonial branch develops by the repeated division of the terminal cell. In several cases the nucleus of this cell is considerably enlarged and is evidently just preparing for division (fig. 28). The chromatophores are much more openly clathrate in the 5-celled carpogonial branch than in the younger branches (fig. 29). One branch was observed in which the fifth cell, the terminal cell, was binucleate (fig. 30). Each cell in a carpogonial branch until it has reached the 5- or 6-celled stage generally contains one chromatophore. The one chromatophore then divides into a number of small parts which are connected by strands of cytoplasm (fig. 31). The structure and the arrangement of the cytoplasm and chromatophores at this stage appear to be very similar to those in the tetrasporangium and the tetraspores. The fate of most of the chromatophores in the cells of the carpogonial branch appears to be the same as that of those in the spermatium mother cells. The chromatophores disappear and at the same time the granular cytoplasmic contents of the cells increase. The protoplasm in the chromatophores is apparently used to form a part of the granular cytoplasm. There are generally present 2 or 3 chromatophores in each of the 3 or 4 basal cells, even after fertilization, when the sporogenous filaments are being formed (fig. 42). These chromatophores are hollow ellipsoids, like those in the tetraspores, but unlike the latter generally show no sign of being clathrate.

A large number of carpogonial branches were observed which bore short stumps or fairly long pieces of trichogynes (figs. 32–38). These trichogynes could often be traced almost to the surface of the thallus (figs. 35, 37). Other trichogynes were found which projected beyond the surface of the thallus and which could be traced back toward carpogonial branches (figs. 39, 40). Although no carpogonial branch was found in which the trichogyne could be traced from the carpogonium out beyond the surface of the thallus,

it is evident that this is actually its course. The failure to obtain a satisfactory section was due to the varying and indirect course of the trichogyne. Though most of the sections examined were 12 μ thick, the trichogyne nearly always passed out of the section and it was very difficult to locate it in the adjoining sections. The trichogyne, just beyond its point of attachment to the carpogonium, is often much coiled (figs. 34, 37, 40). The trichogyne is always surrounded by a fairly thick gelatinous wall which is a continuation of that of the carpogonium (figs. 34, 37). The granular cytoplasmic content of the trichogyne stains with the same intensity as does that of the terminal cells of the carpogonial branch. No structure was seen in any trichogyne which could positively be identified as a nucleus. In a few cases a body was seen which appeared to be similar to a nucleolus (fig. 39). This body is surrounded by a light area, but not by a definite membrane, and is therefore not thought to be a nucleus. There are present in some of the trichogynes (fig. 37) 2 or 3 masses which, with hematoxylin, stain like chromatin. The question of the presence of a nucleus in the trichogyne of the Florideae is still unsettled. SVEDELIUS reports that the trichogyne nucleus in *Delesseria sanguinea* disintegrates before fertilization and the chromatin granules pass out into the cytoplasm. It is possible that some of the granules seen in *Dumontia* and other forms are chromatin granules of similar origin.

There are two types of mature carpogonial branches. A cell is sometimes formed as a lateral outgrowth of the basal cell of the carpogonial branch (fig. 35). The cell thus formed is a supernumerary cell and will not be numbered, as it is not always present and has no special function. This supernumerary cell has never been observed in a carpogonial branch which is not mature. The basal cell of the carpogonial branch is often found to be binucleate (figs. 35, 38, 40) and sometimes contains as many as 3 nuclei (fig. 36). The basal cell is sometimes binucleate after having cut off the supernumerary cell (fig. 35). It thus appears that there is a tendency of the basal cell to form a lateral branch. Also the third cell of some of the carpogonial branches appears to be binucleate (figs. 33, 38). It is difficult to determine whether the nucleus in

these cells has actually divided or has merely elongated. The nuclei of cells 1, 2, and 3 of the carpogonial branch are often not in the resting condition, that is, all the chromatin is not in the nucleolus. The chromatin in these nuclei may be in one body surrounded by a number of small granules (fig. 32, cells 1, 2; fig. 38, cell 1), or in several small bodies (fig. 32, cell 3; fig. 36, cell 3; fig. 37, cell 3). The 3 terminal cells (4–6) are smaller than the first 3 or 4 cells and their nuclei are generally in the resting state. In many of the Delesseriaceae and Ceramiaceae some of the cells of the carpogonial branches contain two or more nuclei. The vegetative cells in these forms are multinucleate, and it is not surprising that this nuclear condition should occur also in cells of the carpogonial branches. In a form like *Dumontia*, where nearly all the vegetative cells are uninucleate, it is surprising that any cells of the carpogonial branch should contain more than one nucleus. However, the cytoplasmic contents of the carpogonial cells are much greater than those of the adjoining vegetative cells in proportion to their size, and the presence of an extra amount of chromatin in the larger cells of the carpogonial branches is quite in accord with the current belief of a definite relation in volume between cell and nucleus. The mature carpogonium lies close to or in contact with the third cell (figs. 32–38).

Only 4 trichogynes with spermatia attached to them were found in all the material examined. These were found in the material collected in April 1915. Although this number is small, it is not less than would be expected, since only a very few trichogynes were found projecting beyond the surface of the thallus. This may have been due to the fact that the mature trichogynes persist for only a short time, or that they are easily broken off. It is to be regretted that none of these trichogynes with the spermatia attached to them could be traced back to the carpogonium. In none of these cases was it possible to find even the carpogonium. In one case one spermatium had fused with the tip of a trichogyne, while 7 others were merely adhering to its sides (fig. 41). Judging from the way it stained, the cytoplasm in this one spermatium and in the tip of the trichogyne had begun to disintegrate. The other spermatia stained very lightly, and it was not possible to

distinguish the structure of their contents. The cytoplasm in all the trichogynes with the spermatia attached to them appeared to be disintegrated, and no trace of a male nucleus was seen in any of them. Disintegrating cytoplasm stains very deeply in vegetative cells which have been injured, in trichogynes which have functioned, in carpogonial branches which have not been fertilized but are destined soon to disappear (fig. 36), and in those cells of the auxiliary cell apparatuses which are terminal and will also soon disappear. The cytoplasm of the trichogyne would not disintegrate as soon as the male nucleus had entered it, so that this nucleus in all these cases had probably passed into the carpogonium. Only one spermatium was attached to each of the other 3 trichogynes.

It has always been extremely difficult to obtain clear evidence concerning the phenomenon of fertilization in the Florideae. A few workers, as OLTMANNS (9), OSTERHOUT (11), HASSENCAMP (3), WOLFE (19), YAMANOUCHI (20), and SVEDELIUS (16) have succeeded in finding consecutive stages showing the fusion of the spermatium to the trichogyne, the passage of the male nucleus down the latter, and the fusion of the male and female nuclei in the carpogonium. The only two members of the Dumontiaceae in which the structure of the female reproductive organs has been carefully worked out are *Dudresnaya purpurifera* and *D. coccinea* (OLTMANNS 9). OLTMANNS in *D. purpurifera* observed the entrance of the male nucleus into the trichogyne. The nucleus of the carpogonium at this time has moved out into the coiled portion of the trichogyne. No nucleus is present in the trichogyne in the next stage which he observed, but in the carpogonium there is a nucleus which he assumes to be the fusion nucleus. OLTMANNS states that he was not able to secure satisfactory evidence concerning the fusion of the male and female nuclei. He does not describe or picture fertilization in *Dudresnaya coccinea*, but states that it is in no way unusual. In *Dumontia* less evidence has been obtained concerning fertilization than OLTMANNS presented in the discussion of the two species of *Dudresnaya*. Nevertheless, there is really no reason to doubt the occurrence of fertilization in these forms.

As previously stated, the mature carpogonial branch is always bent around so that the carpogonium is close to or in actual contact

with the third cell. In many cases it lies very close to the second cell also. Thus the structure of the carpogonial branch suggests that the fusion nucleus passes from the carpogonium into the second or third cell. This evidently does occur, although satisfactory stages showing the process have not been found. Such figures as 42 and 43 show that the sporogenous filaments originate from either the second or third cells of the carpogonial branch. Since the actual passage of the fusion nucleus into the cell producing the sporogenous filaments has not been observed, there will naturally arise a question concerning the origin of the nuclei in these filaments. It cannot positively be stated that the nuclei in the sporogenous filaments are descended from the fusion nucleus of the carpogonium, but most of the evidence leads to this conclusion. Hundreds of carpogonial branches which have not been fertilized have been examined, and in only two or three cases is there any evidence that the third cell is binucleate. The second cell has never been observed to contain more than one nucleus. OLTMANNS (9) states that in *Dudresnaya coccinea* the cell of the carpogonial branch with which the sporogenous filament fuses is often binucleate, but that these nuclei never move out into the sporogenous filaments. Spermatia are found fused to trichogynes projecting beyond the surface of the thallus. Sporogenous filaments are found arising from cells of carpogonial branches whose trichogynes probably had projected beyond the surface of the thallus (fig. 42). The cells which produce the sporogenous filaments are those which in other carpogonial branches are always close to or in contact with the carpogonium. Considering these facts it seems highly probable in *Dumontia filiformis*, as in *Dudresnaya purpurifera* and *D. coccinea*, that the nuclei in the sporogenous filaments are derived from the fusion nucleus in the carpogonium. All the cells in the carpogonial branches stain very faintly at the time of the formation of the sporogenous filaments. The cytoplasm in all the cells, particularly the terminal ones, becomes very thin (fig. 42) and in some cases practically nothing but the cell walls is visible. The cytoplasm in these cells is disintegrating, but not in the same manner as it does in the trichogynes and some of the other cells. The failure to find the carpogonium may be due to the fact that it disintegrates

after it has discharged its nucleus. The carpogonium is much smaller than the cell which produces the sporogenous filaments, so that it might still be present, although not recognizable, after the fusion of the two cells.

The sporogenous filaments in *Dumontia*, according to SCHMITZ (13), grow out from the carpogonium and do not fuse with any cell in the carpogonial branch. This statement obviously is not correct. One cell of the carpogonial branch in *Dumontia* may produce three sporogenous filaments (fig. 42). A mass of fairly dense cytoplasm which always contains a nucleus and sometimes a chromatophore is present at the tip of each filament (fig. 42). The remainder of the filament appears to be entirely empty. The sporogenous filaments in *Dudresnaya purpurifera* (OLTMANNS 9) arise from the carpogonium and do not fuse with any cell in the carpogonial branch. A carpogonial branch in *D. purpurifera* and *D. coccinea* produces 2 or 3 sporogenous filaments. Each of these filaments in *D. coccinea* fuses with a cell of the carpogonial branch before growing out into the tissue of the thallus. All the cytoplasm in the 3 sporogenous filaments in *D. purpurifera* is derived from the carpogonium, in *D. coccinea* from the carpogonium and 3 other cells of the carpogonial branch, and in *Dumontia* from either the second or third cell of the carpogonial branch.

AUXILIARY CELL BRANCHES

The auxiliary cell branches of *Dumontia* have the same origin and the same distribution as the carpogonial branches, but they are not so numerous as the latter. The ratio of carpogonial to auxiliary cell branches, considering the average number of branches initiated on a plant, is approximately 7 to 1. The carpogonial branches are very numerous in certain regions, as at the base of the mature cystocarpic plant. The auxiliary cell branches are found to predominate over the carpogonial branches at slightly higher level on this same plant.

The mature auxiliary cell branches vary in length from 4 to 6 cells (figs. 44, 45). The basal cell, just as in the carpogonial branch, may cut off a supernumerary cell (figs. 43, 45, 46). The size of the cells and the mode of development of the auxiliary cell branch

are essentially similar to those of the carpogonial branch. The youngest auxiliary cell apparatus which could be distinguished from a carpogonial branch consists of 3 cells (fig. 47). The similarity of the two branches is very apparent. The terminal cell of the auxiliary cell apparatus as a rule is not as pointed as that of the carpogonial branch (compare figs. 44–53 with figs. 24–28). There are, however, exceptions to this rule (figs. 48, 54). This cell may not be pointed even when it is about to divide (figs. 52, 53). There is also some difference in the way in which the cytoplasm of the cells of the two branches stains. This difference is so slight that it can be used as a criterion in distinguishing the two kinds of branches only when they are in one section or in sections which have been similarly fixed and stained. The basal cell of the auxiliary cell apparatus is often binucleate (fig. 50) and sometimes contains 3 nuclei (fig. 48), as does the similar cell in the carpogonial branch (fig. 36). None of the cells except the terminal one was ever observed to be binucleate in a carpogonial branch which was not mature. The auxiliary cell branch shown in fig. 49 is not mature, and the second cell is binucleate. Fig. 50 shows an immature branch in which 3 cells are binucleate. Some of the cells in the auxiliary cell branches contain chromatophores similar to those in the cells of the mature carpogonial branches and in the sporogenous filaments (figs. 44, 55). The auxiliary cell is either the second or third cell of the branch (figs. 43, 45, 57–60, 63). The sporogenous filament with the nucleus in its end grows toward the auxiliary cell branch (fig. 54).

The sporogenous filament fuses with the auxiliary cell (figs. 43, 45, 56, 59). Some of the cytoplasm of the sporogenous filament undoubtedly fuses with that of the auxiliary cell. This appears evident from the fact that the end of the sporogenous filament always contains cytoplasm and in some cases terminates in the auxiliary cell (figs. 45, 56, 59). After the fusion of the sporogenous filament with the auxiliary cell, the original nucleus of the latter maintains its former position (figs. 45, 60, 63) or withdraws to one side (fig. 58) as in *Dudresnaya purpurifera* and *D. coccinea*. It has been stated that cells 2 and 3 of the auxiliary cell branch are occasionally binucleate. This binucleate condition in the auxiliary

cell is apparently of no significance, because the nucleus from the sporogenous filament enters here just as it does in the uninucleate auxiliary cell (fig. 57). OLTMANNS reports that the sporogenous filaments in *Dudresnaya purpurifera* and *D. coccinea* branch freely. These filaments in *Dumontia* apparently branch only occasionally (figs. 42, 43). In both species of *Dudresnaya* no septa are formed in the filaments except when they fuse with the auxiliary cells. When the septa do occur, they are formed in the filament on both sides of its point of fusion with the auxiliary cell. The tip of the filament may then grow on to fuse with 2 or 3 more auxiliary cells. In *Dumontia* only one case was observed in which a filament has actually fused with an auxiliary cell and does not also terminate in the cell (fig. 43). No septa were seen in this filament. A few filaments growing over auxiliary cells were observed, but in these cases there was no indication of any fusion (figs. 44, 53). The sporogenous filament in fig. 43 branches just before it terminates in the auxiliary cell.

CYSTOCARPS

Carpospore development is initiated by the formation of 3 or 4 gonimoblast filaments, of about 3 cells each, which arise successively from the lateral protrusion of the auxiliary cell. These filaments branch once, often twice, and every cell forms a spore (figs. 56, 59). The cells at first are uninucleate (figs. 56, 58, 59, 63). At a little later stage they become binucleate and divide (fig. 62). No sterile cells are present at the base of the gonimoblast filaments. The carpospores when first formed are rounded or subangular and about 11 μ in diameter. They are well filled with a spongy cytoplasm which contains many small vacuoles (fig. 63). No chromatophores are visible, but often a number of small dark staining granules are present. When the nucleus is in the resting state, all the chromatin is in the nucleolus. In the young cystocarp there are generally present 3 or 4 cells of the auxiliary cell branch (figs. 56, 58, 63), and sometimes as many as 5 (fig. 62). A portion of the auxiliary cell branch is often present even in the mature cystocarp (fig. 60). The wall of the cystocarp is formed by branches which grow out from these subcortical cells that have been displaced inward by the enlargement of the group of carpospores (fig. 63).

The growth of these branches which form the pericarp is similar to that of the ordinary subcortical branches.

On an average 9 carpospores are present in a median transverse section of a mature cystocarp. Often 3 or 4 cystocarps will crowd together, so that in a section they appear as one. The average diameter of the mature carpospores is 38 μ. When the carpospores are actually mature, they are well filled with cytoplasm, contain a large amount of Floridean starch, and a number of protein granules. These granules respond to the stain and to the protein test in the same way as those in the tetrasporangia. These protein granules when they first appear are small and very numerous. In one carpospore in a median section 12 μ thick there are 170 of these granules (fig. 64). The ringlike chromatophores, about 2.5 μ in diameter, first appear in the carpospore just before it is mature. They are not peripheral but are scattered throughout the entire protoplast. Chromatophores are often present in the sporogenous filaments and in the auxiliary cells, but have never been seen in the latter at the time the carpospores are formed. It is possible that chromatophores which do not take the stain are present in these cells, although it seems hardly probable that they could be completely overlooked, since the cytoplasm in the auxiliary cell is very thin and much vacuolated. It is generally believed that chromatophores never arise *de novo*, and SCHMITZ (12) has stated that they are always present in the spores of the Florideae. In other Florideae besides *Dumontia* the chromatophores are evidently not readily seen at this stage, since their presence in the young carpospores is rarely mentioned.

The protein granules in the mature carpospores often disappear just before the spores are discharged, and are never present in the germinating spores. Certain of the chromatophores increase greatly in their staining power coincident with the disappearance of these granules (fig. 65). There has evidently been some modification in the substance of these chromatophores, and it seems quite possible that the substance of the protein body is concerned with this change. The chromatophores in the mature carpospores which have thus become differentiated stain with the same intensity as those in the germinating carpospores and appear to have the same

structure as those in the mature tetraspores. The majority of carpospores in a mature cystocarp contain one large nucleus each (fig. 66). Occasionally a spore which is just about to escape contains 2 nuclei (fig. 67). The spore shown in fig. 67 was directly behind a spore which was just passing through the pore in the wall of the cystocarp. The fact that the nucleus divides in some of these carpospores just as they are escaping indicates that the spores germinate as soon as they are discharged. In fact, the spores sometimes germinate while still inclosed in the cystocarp. In most of the female plants collected, the tips of the main axis of the thallus and branches were frayed out. The mature carpospores are present at these points, and it is therefore evident that the disintegration of the cells surrounding them furnishes one possible means of escape. As the carpospores enlarge, they compress the surrounding vegetative cells on all sides, and also cause the wall of the thallus to bulge out. The layers of cortical and subcortical cells gradually become thinner on the bulging side of the pericarp, until finally they are ruptured and the naked carpospores escape through the pore thus formed (fig. 68, 1).

Groups of multinucleate cells, which are of the same size and have the same position as the normal cystocarps, occasionally occur in the wall of the thallus. In group 1, fig. 68, a section of a normal cystocarp, 16 spores appear to be present, but probably not all of these are in this one cystocarp. Similar sections of two groups of multinucleate cells on the other side of the thallus (2 and 3) contain respectively 30 and 70 cells. Some of the cells in the groups of multinucleate cells are uninucleate and of the same size as the mature carpospores (fig. 66), while others of approximately the same size or smaller contain 2 or 3 nuclei (figs. 67, 69, 71). In some cases nuclear division is followed by cell division (fig. 70). Evidently after one of these larger spores divides, the daughters may in turn become multinucleate (fig. 71). From the arrangement of some of the cells it appears as though the larger cells have divided to form the smaller ones. The number of nuclei in the cells of a cystocarp similar to group 3, fig. 86, does not seem to be determined by the size of the cells. Some of the smaller cells may contain as many as 11 nuclei and the larger ones only

1 or 2. These are certainly nuclei and not pyrenoids, since they were clearly distinguished by hematoxylin, safranin, or methyl green. Many of these cells are somewhat vacuolated, and none of them contains protein granules or visible chromatophores. No cases have been observed in which any of these cells are escaping from the cavity. It seems probable from all the evidence available that such a group as 3 is formed by division of the spores of a normal cystocarp, and 2 is an intermediate stage between 1 and 3. Each of these groups of multinucleate cells, therefore, is the product of an abnormal cystocarp.

Germination of the carpospores may begin long before they escape from the thallus. The first step in germination is the formation of a gelatinous wall 2 μ thick (fig. 72). The chromatophores in these spores were 3 μ in diameter and stained darkly. They are similar in structure to those in the tetraspore, but are larger and more openly clathrate (figs. 73, 74). The chromatophores are not merely peripheral, but, as in the younger carpospores, are scattered throughout the whole protoplast. The next step in germination is the elongation of the spore until it becomes somewhat pear-shaped (fig. 74). The nucleus then divides and the first cell wall is formed perpendicular to the longitudinal axis of the carpospore (fig. 75). The narrow cell, as in the germinating spores of *Fucus*, is destined to form the basal part of the young plant. Neither growth nor cell division takes place as rapidly here as in the upper cells. The next wall formed apparently divides the upper cell obliquely (fig. 76). In a longitudinal section of an older sporeling these two upper cells were divided into 9 cells and the lower cell into 3 cells. All the cells of these germinating carpospores are rich in cytoplasm and contain chromatophores. The maximum size of the sporelings examined was 235 μ by 123 μ. In cavities containing germinating carpospores traces of disintegrating cytoplasm and nuclei have been observed, showing that some of the unicellular carpospores have degenerated.

CYTOLOGY

The nuclei in the auxiliary cell and the carpogonial branches are the most satisfactory ones in the cystocarpic plants for the study of

mitosis, since they are considerably larger and divide more actively than the vegetative nuclei. The cell history of these branches is also of some aid in identifying stages in nuclear division. All the chromatin in the nuclei of most of the young carpogonial branches is in the nucleolus (figs. 22–30). This is true of the nuclei also in cells 4, 5, and 6 of the mature branches (figs. 32–34, 37). The nuclei in cells 1, 2, and 3 of the mature carpogonial branches have a tendency to divide. The failure to secure any stages of mitosis in the nuclei of the cells of the young carpogonial branches is probably due to the fact that these cells divide very rapidly. The chromatin in the nuclei in most of the uninucleate cells of the mature auxiliary cell branches is not in the nucleolus but in a number of small granules (figs. 48, 51–55). The nuclei in the cells of these branches divide often (figs. 46, 48–50). The frequency of division of these nuclei is probably due, as in the basal cells of the carpogonial branch, to the fact that these cells are usually completely filled with dense cytoplasm (fig. 51). Thus in the resting nuclei of the cells of the carpogonial branches, as in the tetraspores and vegetative cells, all of the chromatin is in the nucleoli.

The following changes are observed in the nuclei in preparation for division. Radial fibrillae appear running from the nucleolus to the nuclear membrane (cell 2, fig. 55). Small chromatin granules pass out from the nucleolus, along the fibrillae, to the nuclear membrane. When the granules first appear on the linin strands, there is no appreciable decrease in the size of the nucleolus. The position of these granules when they first appear indicates that they have come from the nucleolus. Of the 6 granules present in fig. 77, 3 are in contact with the nucleolus, and only 1 has yet reached the periphery of the nucleolus. Nearly all of the granules at a slightly later stage are present only at the points where the fibrillae terminate in the nuclear membrane (fig. 78). More linin strands are formed which connect the radial fibrillae already present (fig. 79). All of the chromatin evidently passes out of the nucleolus and becomes distributed along the linin net. The net disappears just before the nucleus divides (fig. 80). Practically all of the chromatin in the nuclei which have just divided is in 7 fairly uniform granules (cell 4, fig. 52). The nucleus of cell 4,

fig. 53, is evidently just dividing. All of the chromatin in the nucleus of this cell is in 14 granules of approximately the same size. Nuclei which are probably preparing for division often contain 7 similar chromatin bodies (cell 3, fig. 51; cell 4, fig. 55; fig. 81). It is thought that the chromatin bodies in these nuclei may be chromosomes. Nuclei in the earlier stages of division contain 16–24 granules (cells 1 and 3, fig. 52; figs. 79, 80). These granules must become grouped together to form the chromosomes. Thus possibly the haploid number of chromosomes in *Dumontia* is 7. However, it is evident that not enough data have been accumulated to determine with any degree of certainty the number of chromosomes. These larger chromatin bodies in some of the nuclei are vacuolated (cell 3, fig. 51). All the chromatin in the resting nucleus is in the nucleolus, hence the chromosomes must fuse together after division. It is quite possible that all the chromosomes do not fuse at one time. Thus in fig. 82 each of the 2 large chromatin bodies in the nucleus which contains 5 may have been formed by 2 chromosomes fusing together. If the fusing continued, the nucleus would appear quite similar to that in the adjoining cell. When the nucleus is being organized after division, the nucleolus appears granular, and a few small chromatin bodies may, for a time, remain outside of it (fig. 62). In the nucleus of the mature carpospore the linin net is well developed, and all the chromatin is in the nucleolus, which always contains at least one vacuole (fig. 66). Our knowledge of the details of mitosis in this species of *Dumontia* is as yet very fragmentary. The stage represented in cell 3, fig. 52, is similar to the prophase of *Delesseria* as described by SVEDELIUS (15). This cannot be the prophase in *Dumontia* because the granules present at this stage collect together to form larger units, probably chromosomes.

In *Polysiphonia* (YAMANOUCHI 20) and *Delesseria* (SVEDELIUS 15) the chromatin from which the chromosomes are formed is never contained in the nucleolus. It is distributed in fine granules along the linin threads. The granules are in groups or short rows, each one of which represents a prochromosome. A chromosome is then formed by the fusion of several granules. Mitosis in *Dumontia* up to the time of chromosome formation seems to be

exactly similar to that in *Nemalion* (Wolfe 19). Nearly all the chromatin in the resting nucleus of *Dumontia* is in the nucleolus, and, as in *Nemalion* and *Griffithsia* (Lewis 6), this chromatin passes out along the fibrillae to the periphery of the nucleus. The number of granules present in *Griffithsia* and *Nemalion* seems to be about twice the number of chromosomes formed. This may be the case in *Dumontia* also, although in this form the number of granules seems proportionately larger. There is no indication of any chromatin being expelled from the nucleus of *Dumontia* as it is in *Griffithsia*.

Discussion and results

The auxiliary cell branch and carpogonial branch of *Dumontia filiformis* resemble each other very closely in origin, mode of development, and structure. This similarity is so great that in some cases it is almost impossible to determine the character of a branch. The number, arrangement, and contents of the cells may be the same in these two kinds of branches. The trichogyne persists for only a short time after it has functioned. Hence the absence of this structure is not a safe criterion for distinguishing the auxiliary cell branches. The carpogonial and auxiliary cell branches differ greatly from the vegetative branches in the size and contents of their cells. It seems quite possible that the auxiliary cell branches in *Dumontia* once bore trichogynes and functioned as carpogonial branches. This similarity in structure of the auxiliary cell and carpogonial branches is almost as marked in *Dumontia* as in *Dudresnaya coccinea*. The auxiliary cell branch of *D. coccinea* consists of 12 cells and the carpogonial branch of 7 cells (Oltmanns 9); otherwise the two kinds of branches appear similar in origin and structure and differ greatly from the vegetative branches.

It has been stated that the auxiliary cell branches and carpogonial branches of *Dumontia* are probably homologous structures. If this is true, the sporogenous filaments were probably developed at the time when certain carpogonial branches ceased to be capable of fertilization. The male plants in this species of *Dumontia* are present for only 2 or 3 weeks during each spring. The ratio of the number of female to male plants at the time when the latter are supposed to be at the height of their development is 3 to 1.

An examination of scores of young female plants has shown that the trichogynes must persist for only a short time after they have reached the surface of the thallus. Under these conditions an arrangement whereby the fertilization of one carpogonium would make possible the development of 3–6 cystocarps would evidently be of considerable advantage to the plant. If the auxiliary cell branches are carpogonial branches which have ceased to function, *Dumontia* presents a case quite parallel to that of *Corallina*. In *Corallina* (OLTMANNS 10) only those carpogonia in the center of the conceptacle which bear long trichogynes are capable of being fertilized. The carpogonia at the periphery of the conceptacle cannot be fertilized because they bear no trichogynes. In each conceptacle often only one carpogonium is fertilized. Descendants of the fusion nucleus in this one carpogonium pass to the auxiliary cells of many procarps, and several cystocarps develop in one conceptacle.

Cell 2 or 3 of the carpogonial branch of *Dumontia* probably functioned as the auxiliary cell before the plant had acquired the habit of forming sporogenous filaments. It is cell 2 or 3 of the auxiliary cell branch which forms the carpospores. One of the 3 cells in the carpogonial branch of *Dudresnaya coccinea* with which the sporogenous filaments fuse, before passing to the auxiliary cell branches, at one time probably functioned as the auxiliary cell. The sporogenous filament often fuses with the fifth cell of the carpogonial branch and with the fifth cell of the auxiliary cell branch. In both *Dumontia* and *Dudresnaya coccinea*, therefore, that which is supposed to have been the original auxiliary cell and that which now functions as such occupy similar places in their respective branches. The families of the Cryptonemiales show a considerable variation in the distribution and structure of their auxiliary cell and carpogonial branches. Even the species in one genus as *Dudresnaya* (OLTMANNS 9) may vary greatly in this respect. It would then be rather surprising to find that the history of the development of the auxiliary cells in all the Cryptonemiales is similar. OLTMANNS (9) suggests that the sporogenous filaments of the Cryptonemiales have been developed from the gonimoblast filaments of such forms as *Wrangelia* and *Naccaria*. He considers

Nemastoma the transitional form between the Nemalionales and the Cryptonemiales. The auxiliary cells of *Nemastoma* do not occur in special branches, but are modified cells of the cortical hyphae. Thus in *Nemastoma* there are no auxiliary cell branches which can be considered as homologous with the carpogonial branches. But there is also the evidence which has been presented that the auxiliary cell branches in some forms as in *Dumontia* are not vegetative hyphae which have by chance become highly specialized in the same manner as the carpogonial branches. Thus the sporogenous filaments, structures which are peculiar to this one order, the Cryptonemiales, have probably been developed along two independent lines.

The female reproductive organs of the other red algae are relatively simple when compared with those of the Cryptonemiales. It is not surprising that the history of the nuclei in the sporogenous filaments and auxiliary cells of the members of this order was an especially puzzling problem to the earlier students. It has been stated in the introduction to this paper that the origin of the nucleus functioning in the auxiliary cells at the time of the formation of the carpospores proved to be a stumbling block to most of these students. The results of the work of SCHMITZ on certain genera of the Cryptonemiales, including *Dudresnaya*, *Dumontia*, and *Gloeosiphonia*, were conflicting in regard to the occurrence of a fusion between the sporogenous and auxiliary cell nuclei. OLTMANNS' (9) investigation established practically beyond doubt the two following facts: the sporogenous and auxiliary cell nuclei in *Dudresnaya* and *Gloeosiphonia* do not fuse, and the nuclei in the carpospores are descended from the sporogenous nucleus and not from the original auxiliary cell nucleus.

No member of the Cryptonemiales has been carefully investigated since 1898 in regard to the occurrence of a nuclear fusion in the auxiliary cell. A considerable amount of excellent work, however, has been done on other red algae during the last 17 years. The fusion nucleus or one of its daughters, in many genera, has been traced from the carpogonium into the auxiliary cell. The fusion nucleus in all these forms appears to take charge of the cytoplasm in the auxiliary cell and becomes the ancestor of the nuclei

in the carpospores. In none of these forms is the nucleus in the auxiliary cell reported to fuse with the nucleus entering it from the carpogonium. Thus HASSENCAMP (3), YAMANOUCHI (20), SVEDELIUS (14), and LEWIS (6) have found, in the forms studied by them, that only one nuclear fusion occurs during fertilization and the formation of the carpospores, and this is the fusion between the nucleus of the spermatium and that of the carpogonium. It would seem that the evidence is overwhelming against the occurrence of a second fusion in the auxiliary cell. Undoubtedly one reason why OLTMANNS' work has been questioned is the fact that certain morphologists have for years cherished the theory that a relationship could be established between the Ascomycetes and the Florideae. The ascogonium of certain genera is remarkably similar in structure to the carpogonium of some of the Florideae. No other plants except those belonging to these two classes have this kind of a female reproductive organ. According to some workers, certain genera of the Ascomycetes are distinguished from all other plants by the fact that two distinct nuclear fusions occur during fertilization and the formation of the spores. If it could be shown that a second nuclear fusion does actually occur in the auxiliary cell of such a form as *Dudresnaya* or *Dumontia*, the carpogonium with its trichogyne and long sporogenous filaments with the carpospores at their extremities might be proved to be homologous with the ascogonium of some form like *Pyronema* with its trichogyne and long ascogenous hyphae bearing ascospores.

It has been stated that in all probability the nuclei in the sporogenous filaments of *Dumontia* are descended from the fusion nucleus in the carpogonium. However, more evidence is to be desired in regard to the origin of these nuclei. The sporogenous nuclei in *Dudresnaya purpurifera*, *D. coccinea*, and *Gloeosiphonia* (OLTMANNS 9) are unquestionably derived from the fusion nucleus in the carpogonium. In *Dumontia*, as in the 3 species of the Cryptonemiales studied by OLTMANNS, there can be no doubt in regard to the passage of a nucleus from a sporogenous filament into an auxiliary cell. A nucleus is always present in *Dumontia* at the tip of each filament. Tips of filaments are found lying quite near the auxiliary cells. A similar filament is found fused to the auxiliary

cell, and no nucleus is then present in the filament. There are, however, two widely separated nuclei in the auxiliary cell itself, and one of these lies quite near the point of fusion of the filament and the cell. The sporogenous nucleus in *Dudresnaya purpurifera*, *D. coccinea*, and *Dumontia filiformis* at no time even closely approaches the original auxiliary cell nucleus. The 2 nuclei in all 3 species lie at almost opposite ends of the cell. The carpospores are budded off from that end of the auxiliary cell which contains the sporogenous nucleus. In *Dumontia* the original auxiliary cell nucleus and the descendant of the sporogenous nucleus could be identified in nearly all the auxiliary cells which bore carpospores. OLTMANNS (9) observed in *Gloeosiphonia* and *Dudresnaya* several cases of "blind fusion" where, although a sporogenous filament had fused with an auxiliary cell, no nucleus had passed over and the auxiliary cell contained only its own nucleus. No examples of "blind fusion" were found in *Dumontia*. It would seem that OLTMANNS' statement that it is a daughter of the sporogenous nucleus in *Gloeosiphonia* which moves into the pericentral cell might be questioned. The two daughters of the auxiliary cell nucleus and the sporogenous nucleus always lie close together. One of these 3 nuclei divides and one of the daughters moves into the pericentral cell. In *Dudresnaya purpurifera*, *D. coccinea*, and *Dumontia* there can be no question as to the origin of the nuclei in the carpospore. They are derived from the sporogenous nucleus.

Summary

Dumontia filiformis, during May, June, and the first half of July, grows in abundance in the tide pools and on the bed rock at South Harpswell, Maine. This alga became established on the coast at South Harpswell between 1905 and 1913. Antheridial, cystocarpic, and tetrasporic plants may have essentially identical size and vegetative structure. The average size of the antheridial plants is a little less than that of the other plants. Cystocarpic and tetrasporic plants are found growing together on the same rock and in the same tide pools. Female plants which bear mature cystocarps are easily recognized by the protrusions which these form in the wall of the thallus. The type of branching varies

considerably. All male and female plants collected were branched. Tetrasporic plants, simple and branched, were found. The maximum number of branches observed on any individual plant was 30. The color of the plants varies from dark red to pale reddish yellow. Male plants bearing mature spermatia are present in the early part of April and two weeks later have almost completely disappeared. Young female plants were found on April 12, and these reach their maximum stage of development about the middle of May. Tetrasporic plants are most abundant in the latter part of June and have almost entirely disappeared by the first of August. *Dumontia* at South Harpswell must persist through the winter in the form of sporelings developed from the tetraspores.

The vegetative structure is of a type occurring in many families of the Florideae. The disk-shaped holdfast is composed of a single layer of horizontal filaments, each cell of which produces a vertical ascending branch. Certain of these branches elongate to form the medullary hyphae of the tubular thallus. Each medullary hypha has its own initial cell. Every cell of each medullary hypha produces a radial branch. These radial branches, by repeated dichotomous forking, form the subcortex and the cortex. Growth is apical throughout the entire thallus. All the other vegetative cells, except the trichomes, are uninucleate and contain one chromatophore each. All the chromatin in the resting nucleus is in the nucleolus. The chromatophore is a clathrate hollow ellipsoid, lying just inside the cell wall.

The tetraspores are imbedded in the wall of the thallus, and are distributed evenly throughout practically the entire length and circumference of the branches and main axis. Younger tetrasporangia are found toward the base of the plant. The larger subcortical cells become modified to form the tetrasporangia. The chromatophore becomes constricted at intervals, so that it appears to consist of rows of small irregular plates. These bodies persist through all stages of the tetrasporangium, and their number is increased in the tetraspores. No spindle or spireme was seen. The chromatin in some of the nuclei is in several small bodies, but these do not resemble chromosomes. The first cleavage furrow completely divides the tetrasporangium, is perpendicular

to its longitudinal axis, and is parallel to the surface of the thallus. The chromatophores in the tetraspores are hollow, oval bodies with perforated walls. The mature tetraspores do not round off while imbedded in the thallus. They escape either by the disintegration of the cells surrounding them or by a pore formed in the wall of the thallus.

The spermatia form a continuous layer over nearly the entire surface of the thallus. The spermatium mother cells terminate the branches forming the cortex and subcortex. The chromatophore which is present in the young spermatium mother cell partially or completely disappears as this cell matures. The protoplasm which was in the chromatophore is used in forming the granular cytoplasm of the mature cell. The youngest spermatium mother cells observed were binucleate. The first spermatium is cut off diagonally. The mother cell may again become binucleate and cut off a second spermatium in a similar manner on the side opposite to that on which the first was formed. The second spermatium may be formed while the first one is still attached to the mother cell. No chromatophore is present in the spermatium. The nucleus is situated at the distal end of the spermatium in a dense mass of cytoplasm. The proximal end is vacuolated. The spermatium is cut off from the mother cell as a cell and not as a naked protoplast.

The distribution of carpogonial branches in the young female plants is general, as in the case of the tetrasporangia in the tetrasporic plants. The carpogonial branch develops by apical growth and arises as a lateral outgrowth of a large subcortical cell. A mature carpogonial branch consists of 6 or 7 cells and a trichogyne (6 cells always lie in a row). The basal cell ("cell 1") sometimes divides to form a lateral cell. The carpogonium in a mature branch is always close to or in contact with "cell 2" or "cell 3." The sporogenous filaments always arise from one of these two cells. Only a few trichogynes were found projecting beyond the surface of the thallus. Spermatia were found fused to 4 trichogynes.

Each carpogonial branch which has been fertilized produces 2 or 3 sporogenous filaments, all of which arise from one cell. It is thought that the nuclei in these filaments are descended from

the fusion nucleus in the carpogonium. The sporogenous filaments grow out toward the auxiliary cell branches. The auxiliary cell branches in origin, distribution, structure, and mode of development are very similar to the carpogonial branches. Only about 1 auxiliary cell branch is initiated to every 7 carpogonial branches. The time of initiation of the former is a little later than that of the latter. The mature auxiliary cell branch consists of 4–7 cells. The second or third cell of the branch is the auxiliary cell, the cell with which the sporogenous filament fuses and the one which forms the carpospore. The original nucleus in the auxiliary cell takes no part in the formation of the carpospores. The nuclei in the carpospores are descended from the nucleus which enters the auxiliary cell from the sporogenous filament.

In the development of the carpospores and cystocarps 3 or 4 gonimoblast filaments arise from the auxiliary cell. Every cell of these filaments forms a spore. There are about 20 carpospores in each cystocarp. The pericarp is formed by radial branches similar to those which form the subcortex and cortex of the wall of the thallus. Mature carpospores are usually uninucleate, well filled with a cytoplasm, and contain chromatophores. The chromatophores are similar to those of the vegetative cells. The nucleus sometimes divides just as the carpospore is about to escape. Naked carpospores escape through a pore formed in the pericarp. Carpospores sometime germinate while in the cystocarp. The ends of branches of mature plants fray, and this disintegration of cells surrounding the cystocarp furnishes one means of escape for the carpospores and sporelings.

In the resting nucleus of *Dumontia* all the chromatin is in the nucleolus. The nucleolus often contains a vacuole. The chromatin in preparation for mitosis passes out of the nucleolus and in the form of small granules becomes distributed along the linin net. The net disappears and the granules become massed together to form larger units, chromosomes. The number of chromosomes was not definitely determined, but was apparently about 7. No spireme or spindle was seen. After division, the chromatin is again found massed together in the nucleolus.

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LITERATURE CITED

1. Greville, R. H., Algae Britannicae. Edinburgh. 165. 1830.
2. Harvey, W. H., Phycologia Britannica. London. 1846.
3. Hassencamp, A., Über die Entwickelung der Cystocarpien bei einigen Florideen. Bot. Zeit. **60**:65–86. 1902.
4. Hauptfleisch, P., Die Fruchtentwickelung der Gattungen *Chylocladia*, *Champia*, und *Lomentaria*. Flora **50**:307–367. 1892.
5. Kützing, F. T., Phycologia Generalis. Leipzig. 1843.
6. Lewis, I. F., The life history of *Griffithsia Bornetiana*. Ann. Botany **23**:639–690. 1909.
7. ———, Alternation of generations in certain Florideae. Bot. Gaz. **53**:233–246. 1912.
8. ———, The seasonal life-cycle of some red algae at Woods Hole. Plant World **17**:1–35. 1914.
9. Oltmanns, F., Zur Entwickelungsgeschichte der Florideen. Bot. Zeit. **56**:99–141. 1898.
10. ———, Morphologie und Biologie der Algen. Jena **1**:538–599. 1904.
11. Osterhout, W. J. V., Befruchtung bei *Batrachospermum*. Flora **87**:109–115. 1900.
12. Schmitz, F., Die Chromatophoren der Algen. Bonn. 1882.
13. ———, Untersuchungen über die Befruchtung der Florideen. Sitzungsb. d. Königl. Akad. Berlin 215–259. 1883.
14. Svedelius, Nils., Über den Bau und die Entwicklung der Florideen-Gattung *Martensia*. Königl. Svensk. Vet. Akad. Handl. **43**: pp. 101. 1908.
15. ———, Über den Generationswechsel bei *Delesseria sanguinea*. Svensk. Bot. Tidsk. **5**:260–324. 1911.
16. ———, Über die Spermatienbildung bei *Delesseria sanguinea*. Svensk. Bot. Tidsk. **6**:239–265. 1912.
17. Thuret, G., Études phycologiques analyses d'Algues marines. Paris. 1878.
18. Wille, N., Beiträge zur Entwickelungsgeschichte der physiologischen Gewebesyteme bei einigen Florideen. Nov. Act. Leopold. Carolin. Akad. Nat. **52**:51–100. 1888.
19. Wolfe, J. J., Cytological studies on *Nemalion*. Ann. Botany **18**:608–628. 1904.
20. Yamanouchi, S., The life history of *Polysiphonia violacea*. Bot. Gaz. **17**:401–449. 1906.

EXPLANATION OF PLATES XIX–XXII

Lettering of figures.—*aux.n.*, auxiliary cell nucleus; *chr.*, chromatophore; *cps.*, carpospores; *m.h.*, medullary hyphae; *p.g.*, protein granule; *sbc.c.*, subcortical cell; *s.c.*, supernumerary cell; *sp.fil.*, sporogenous filament; *sp.n.*,

sporogenous nucleus; *spm.m.c.*, spermatium mother cell; *st.c.*, stalk cell; *tr.*, trichogyne.

PLATE XIX

FIG. 8.—Vertical section through holdfast showing horizontal hypha and vertical ascending, dichotomously branched hyphae; ×355.

FIG. 9.—Slightly diagrammatic; vertical section through base of plant and holdfast; ×170.

FIG. 10.—Longitudinal section through wall of thallus showing radial hyphae arising as branches of longitudinal, medullary hyphae; ×700.

FIG. 11.—Longitudinal section through apex of young branch; ×340.

FIG. 12.—Surface view of subcortical cell showing structure of chromatophore; ×1000.

FIG. 13.—Longitudinal section through an intercellular connection showing granules of which disk is composed; ×700.

FIG. 14.—Longitudinal section through an intercellular connection, between 2 carpospores, in which granules have not yet become grouped together to form disks; ×1000.

FIG. 15.—Transverse section through wall of thallus of male plant showing stalk cells, spermatium mother cells, and spermatia; ×1000.

FIG. 16.—Longitudinal section through binucleate spermatium mother cell; ×1400.

FIG. 17.—Similar section; spermatium mother cell which has budded off one spermatium; ×1400.

FIG. 18.—Transverse section through wall of male plant showing free spermatia imbedded in gelatinous sheath of thallus; ×1000.

FIG. 19.—Longitudinal section through spermatium mother cell and spermatium; chromatophore at base of spermatium mother cell; ×1400.

FIG. 20.—Longitudinal section through wall of thallus showing origin of carpogonial branches; ×355.

FIGS. 21, 22.—Longitudinal section of first cell of carpogonial branch, showing mode of origin from subcortical cell; chromatophore is similar to those of vegetative cells; ×1000.

FIG. 23.—Longitudinal section of a 2-celled carpogonial branch; ×1000.

FIG. 24.—Similar section of a 3-celled carpogonial branch; ×1000.

FIG. 25.—Longitudinal section of a 3-celled carpogonial branch; ×1000.

FIG. 26.—Similar section of a 4-celled carpogonial branch showing that number of cells is increased by division of terminal cell; ×1000.

FIG. 27.—Similar section of a 4-celled carpogonial branch showing that branches at this stage may be bent to form a right angle; ×1000.

FIG. 28.—Four-celled carpogonial branch; nucleus in terminal cell contains 7 chromosomes (?); ×1000.

FIG. 29.—Five-celled carpogonial branch showing position and structure of chromatophores; ×1000.

PLATE XX

FIG. 30.—Similar carpogonial branch; terminal cells binucleate; ×1000.

FIG. 31.—Section of fifth cell of a 6-celled carpogonial branch; 26 chromatophores distributed on the cytoplasmic net; ×1400.

FIG. 32.—Six-celled mature carpogonial branch showing carpogonium lying near cell 3; ×1000.

FIG. 33.—Similar to fig. 32; cell 3 is binucleate; ×1000.

FIG. 34.—Six-celled carpogonial branch showing coiled trichogyne; ×1000.

FIG. 35.—Seven-celled carpogonial branch showing trichogyne reaching almost to surface of thallus; ×1000.

FIG. 36.—Six-celled carpogonial branch showing carpogonium in contact with cell 3; cell 1 contains 3 nuclei; cytoplasm in cells 4, 5, and 6 is beginning to disintegrate; ×1000.

FIG. 37.—Six-celled carpogonial branch showing much coiled trichogyne reaching almost to surface of thallus; ×1000.

FIG. 38.—Six-celled carpogonial branch showing carpogonium in contact with cell 3 which is much enlarged, nucleus of which is preparing to divide; ×1000.

FIGS. 39, 40.—Base of carpogonial branch, and trichogyne projecting beyond surface of thallus; ×1000.

FIG. 41.—Base of carpogonial branch (cells 1–4), and trichogyne projecting beyond surface of thallus; 8 spermatia attached to trichogyne; ×1000.

FIG. 42.—Carpogonial branch; 3 sporogenous filaments arising from cell 2; ×1000.

FIG. 43.—Carpogonial branch and auxiliary cell branch connected by sporogenous filaments; auxiliary cell branch consists of 6 cells; ×700.

PLATE XXI

FIG. 44.—Auxiliary cell branch; sporogenous filaments lying over cell 4; ×1000.

FIG. 45.—Auxiliary cell branch; sporogenous filament fused with cell 3; ×1000.

FIG. 46.—Auxiliary cell branch; cells 2 and 3 binucleate and a supernumerary cell present; ×1000.

FIG. 47.—Three-celled auxiliary cell branch; ×1000.

FIG. 48.—Five-celled auxiliary cell branch; nucleus of cell 4 preparing to divide; cell 1 contains 3 nuclei; ×1000.

FIG. 49.—Auxiliary cell branch consists of 4 cells; cell 2 binucleate; ×1000.

FIG. 50.—Four-celled auxiliary cell branch; cells 1, 3, and 4 binucleate; ×1000.

FIG. 51.—Four-celled auxiliary cell branch showing dense cytoplasmic contents of cells; 7 chromosomes and colorless nucleolus in nucleus of cell 3; ×1000.

FIG. 52.—Four-celled auxiliary cell branch; part of chromatin in nuclei of cells 1 and 3 in granules distributed on linin net; cell 4 contains 2 nuclei; ×1000.

FIG. 53.—Four-celled auxiliary cell branch; sporogenous filaments lying under cell 3; ×1000.

FIG. 54.—Sporogenous filament lying near 4-celled auxiliary cell branch; ×550.

FIG. 55.—Auxiliary cell branch showing structure of chromatophores; ×1000.

FIG. 56.—Auxiliary cell branch; 5 carpospores budded off from auxiliary cell; sporogenous filament fused with auxiliary cell; ×1000.

FIG. 57.—Auxiliary cell branch; auxiliary nucleus has divided; sporogenous nucleus has just entered auxiliary cell; ×1000.

FIG. 58.—Section through auxiliary cell branch and 8 young carpospores; auxiliary nucleus and sporogenous nucleus at opposite ends of auxiliary cells; ×1000.

FIG. 59.—Section through auxiliary cell branch and group of young carpospores; auxiliary cell and one carpospore shaded; sporogenous filament fused with auxiliary cell; ×1000.

FIG. 60.—Section through auxiliary cell branch and group of mature carpospores; auxiliary nucleus and sporogenous nucleus at opposite ends of auxiliary cell; ×550.

PLATE XXII

FIG. 61.—Same sporogenous filament as in fig. 75 showing cytoplasm nucleus and chromatophore at tip; ×1000.

FIG. 62.—Section through young cystocarp; 2 of the 18 carpospores which have arisen from auxiliary cells binucleate; ×1000.

FIG. 63.—Section through young cystocarp showing origin of radial branches which will form pericarp; ×350.

FIGS. 64, 65.—Partly shaded; sections of mature carpospores showing structure of nuclei, distribution of chromatophores, and protein granules; ×1000.

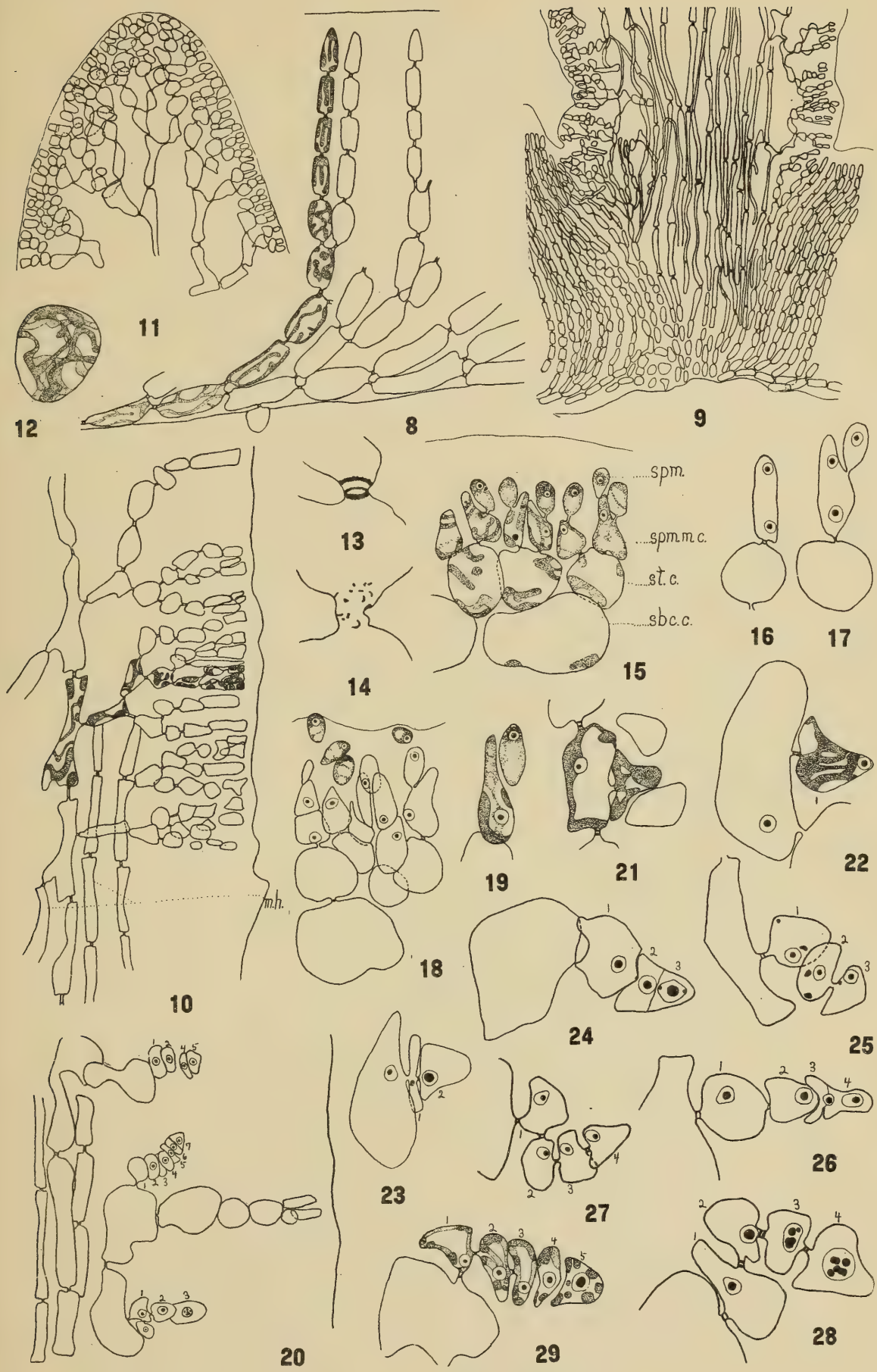
FIGS. 66, 67.—Sections of carpospores in a mature cystocarp; spores of same size and exactly similar to those which occur in abnormal cystocarps; ×700.

FIG. 68.—Transverse section of thallus showing 3 normal and 2 abnormal cystocarps; ×350.

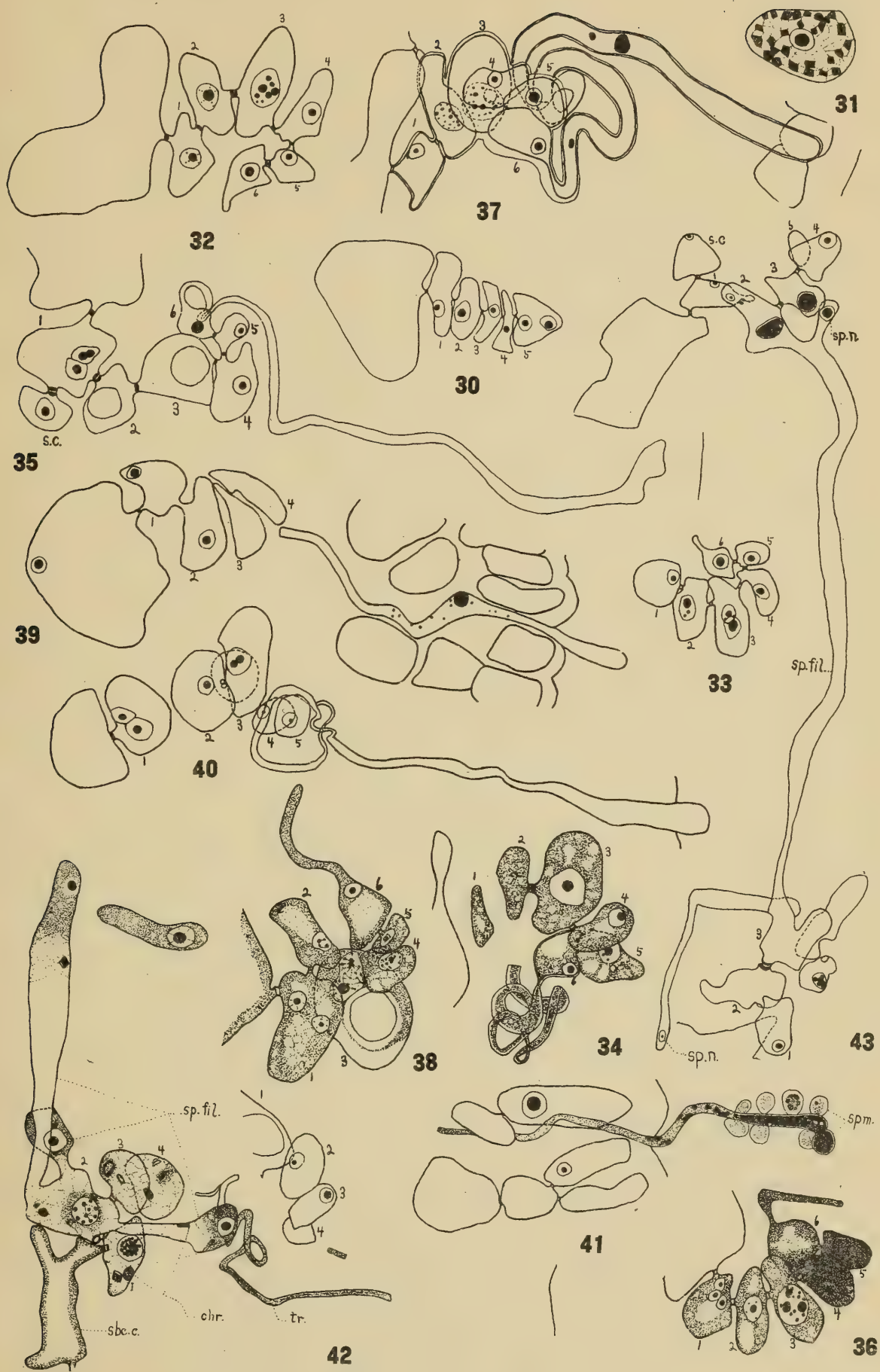
FIGS. 69, 70, 71.—Sections through carpospores in abnormal cystocarps showing that nuclear division is not always directly followed by cell division; ×700.

FIG. 72.—Section of germinating carpospore showing cell wall; ×170.

FIG. 73.—Chromatophores of germinating carpospores; ×1400.



DUNN on DUMONTIA



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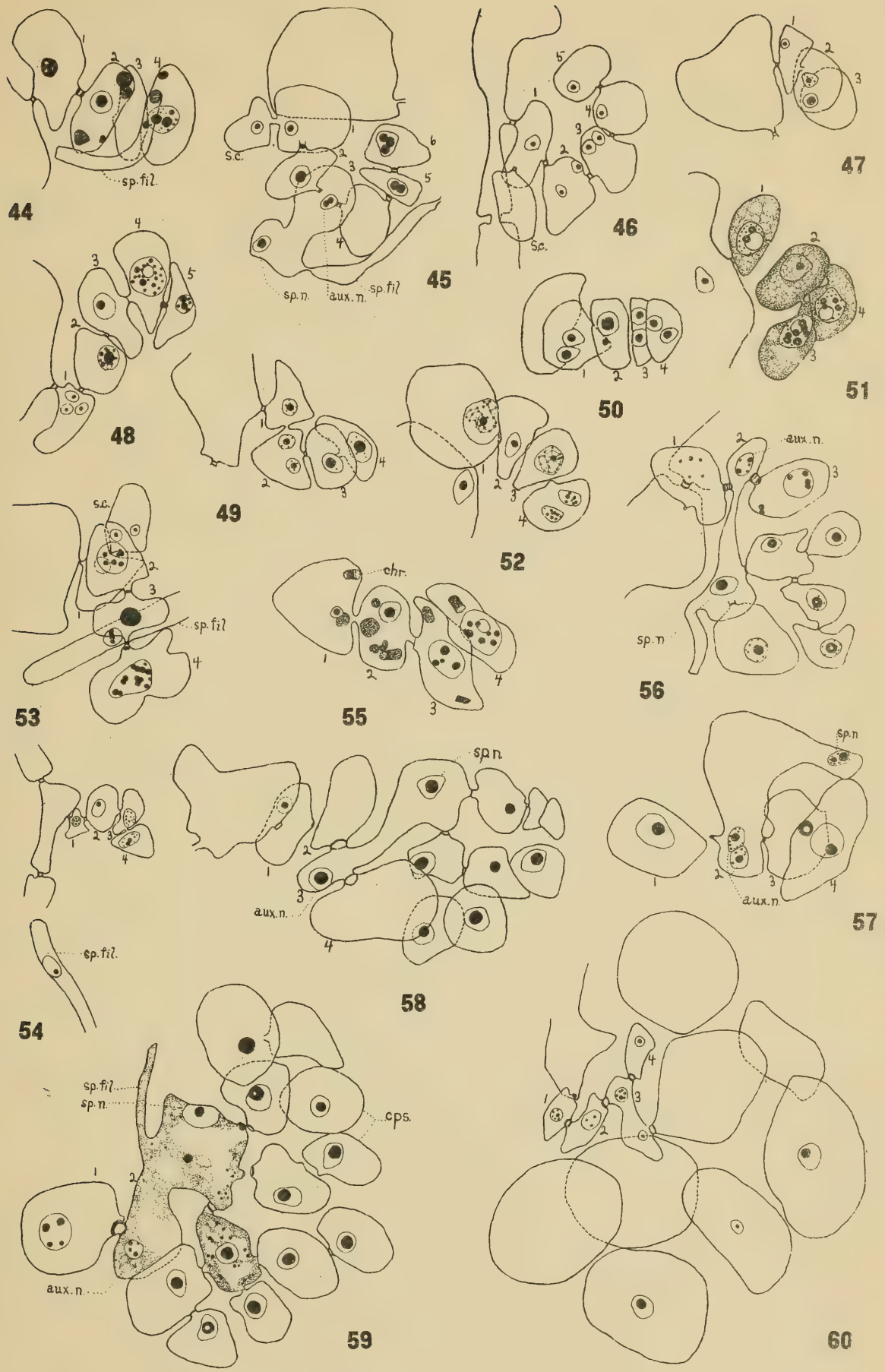
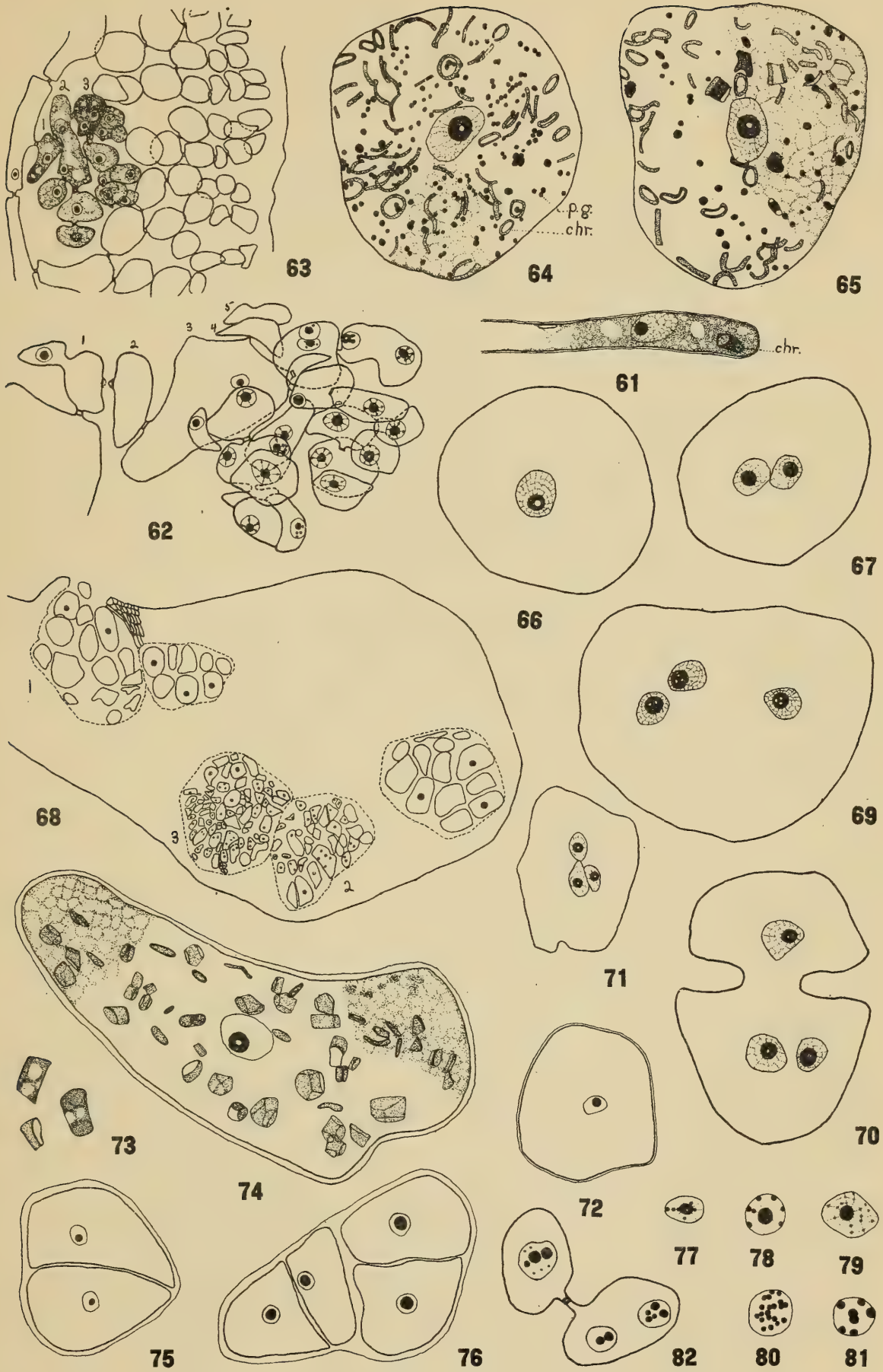


DUNN on DUMONTIA



DUNN on DUMONTIA

FIG. 74.—Partly shaded; longitudinal section of germinating carpospore showing structure and distribution of chromatophores and structure of cytoplasm; ×1000.

FIGS. 75, 76.—Sections of germinating carpospores showing sequence of cell walls during germination; ×170.

FIG. 77.—Nucleus of cell 3 of auxiliary cell branch showing chromatin granules passing from nucleolus to periphery of nucleus; ×1400.

FIG. 78.—Nucleus of cell 3 of auxiliary cell branch showing chromatin granules at periphery of nucleus; ×1400.

FIG. 79.—Nucleus of cell 3 of a carpogonial branch; small chromatin granules present on linin net; ×1400.

FIG. 80.—Nucleus of cell of an auxiliary cell branch; chromatin in small granules; no nucleolus or linin net present; ×1400.

FIG. 81.—Nucleus of cell 1 of a carpogonial branch showing 7 bodies which may be chromosomes; ×1400.

FIG. 82.—Section of 2 cells of an auxiliary cell branch showing chromatin granules in nuclei; ×1000.

VITA

Grace Adelaide Dunn was born at Princeton, Minnesota, on May 1, 1890. She attended Hamline University from 1905 to 1909, receiving the degree of Ph.B. in 1909. She was a graduate student in Johns Hopkins University from 1911 to 1915. In this university her principal subject was Botany and her subordinate subjects were Plant Physiology and Physics. She held a University Scholarship during the years 1913–1914 and 1914–1915.